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Elevated CO_2 enhances productivity and the C/N ratio of grasses in the Colorado shortgrass steppe

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ABSTRACT
Atmospheric CO_2 concentrations have been increasing since the industrial revolution, and are projected to double within this century over today's concentration of 360 µmol mol^{-1}. This study used six open-top chambers in the Colorado, USA shortgrass steppe to investigate how increasing CO_2 will affect productivity and C and N status of indigenous perennial grasses and forbs. From March until October, chambers were placed on two plots in each of the three blocks. In each block, one chamber was assigned an ambient CO_2 treatment (~360 µmol mol^{-1}), the other an elevated CO_2 treatment (~720 µmol mol^{-1}). Each block also had an unchambered control plot. Growth under elevated CO_2 increased above-ground phytomass an average 31% in 1997 and 47% in 1998, with no differences in relative growth responses of C_3 and C_4 grasses and forbs. Growth in chambers was greater than non-chambered control plots, presumably due to warmer temperatures in chambers and a longer growing season. Shoot N concentrations were reduced 21% and C/N ratios increased 23% in elevated compared to ambient chambers. Variation in aboveground phytomass due to year, CO_2 and chamber effects correlated well to % shoot N and C/N ratios, although for both traits different regression lines were required for green plant material (harvested in July) and senescent plant material (harvested in October). Results suggest increased growth and reduced N concentrations in this mixed C_3/C_4 grassland in an elevated CO_2 environment.

KEYWORDS: Global change, C_3, C_4, grassland

INTRODUCTION
Atmospheric CO_2 concentrations have increased from approximately 280 µmol mol^{-1} in the late 19th century to over 360 µmol mol^{-1} today, and are projected to double over present concentrations by the mid- to late-21st century (Alcamo et al., 1996). Most plants exhibit greater productivity with increases in CO_2 above present atmospheric concentrations (Porter, 1993). In a literature review, Wand et al. (1999) showed a doubling of CO_2 to non-domesticated Poaceae enhanced productivity by 33% in C_4 species and 44% in C_3 species. Elevated CO_2 also resulted in increased leaf carbohydrates and decreased N concentrations, but only among the C_3 species. In long-term experiments conducted in the C_4-grass dominated Kansas tallgrass prairie, elevated CO_2 was found to enhance productivity, but only in years with significant water stress (Owensby et al., 1999). Leaf N concentrations were lower in some tallgrass species as a result of growth at elevated CO_2 (Owensby et al., 1993). Our study investigates the consequences of a doubling of CO_2 over present ambient concentrations on above-ground productivity and concentrations of C and N in C_3 and C_4 grasses in the semi-arid Colorado shortgrass steppe.

MATERIAL AND METHODS
The study site is at the USDA-ARS Central Plains Experimental Range (CPER), lat. 40° 50' N, long. 104° 42' W, elevation 1651 m, in the shortgrass steppe region of north-eastern Colorado. Mean annual precipitation averages 320 cm, with the majority occurring during May, June and July. The dominant species is *Bouteloua gracilis* (H.B.K.) Lag. (blue grama), a warm season, C_4 grass. Other important cool season, C_3 grasses include *Pascopyrum smithii* (Rydb.) A. Love (western wheatgrass) and *Stipa comata* Trin and Rupr. (needle-and-thread grass). The soil at the experimental site is a Remment fine sandy loam (Ustollic camborthids).

The effect of elevated CO_2 on this native ecosystem was investigated in 1997 and 1998 using six open top chambers (4.5 m diameter, enclosing 15.5 m^2). From late March until mid-October, chambers were placed on two plots in each of three blocks. Each block had one ambient CO_2 chamber (~360 µmol mol^{-1}), an elevated CO_2 chamber (~720 µmol mol^{-1}), plus an unchambered control plot.

Twice a year, once in late July (peak standing crop) and once in late October (senescence), above-ground vegetation in twenty-eight different 40.5 X 15.3 cm quadrats (1.73 m^2 total) was clipped to the crown, separated by species, dried at 60 °C and weighed. Total shoot C and N analyses were conducted on an automated combustion C/N analyzer (Europa Scientific, Crewe, UK) coupled to an isotope ratio mass spectrometer (Europa Scientific Model 20/20, Crewe, UK). Thirty-six species were found in the chambers, but data were pooled into total above-ground phytomass for this report.

RESULTS AND DISCUSSION
In both 1997 and 1998, production was similar in July and October harvests (Table 1), indicating that peak seasonal above-ground production had occurred by late July. In both years rainfall was above normal (562 and 422 mm in 1997 and 1998 vs. a long-term average of 320 mm), but dry periods lasting from mid-summer through early autumn resulted in no significant growth after July (data not shown).

Table 1 - Effects of CO_2 and chambers on above-ground phytomass (AGP).

Year/Month	Treatments	AGP[1] (g m^{-2} ground area)
1997/July	Control	91 a
	Ambient	112 a
	Elevated	144 b
1997/October	Control	78 a
	Ambient	116 ab
	Elevated	155 b
1998/July	Control	106 a
	Ambient	141 b
	Elevated	203 c
1998/October	Control	86 a
	Ambient	143 b
	Elevated	214 c

[1]Data are means of three replications. F-tests revealed significant ($p<0.05$) treatment effects for all four data sets. Means followed by different letters are statistically different at the $p<0.05$ level (Fisher's LSD).

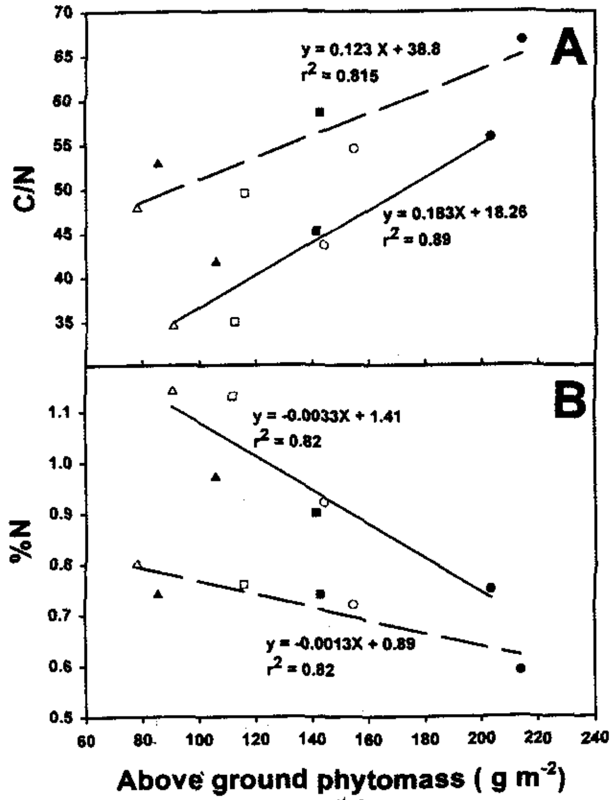

Figure 1 - Variation in shoot C/N (panel A) and %N (panel B) with aboveground phytomass from shoots harvested in July (solid lines) and October (broken lines) in 1997 (△ Control; □ Ambient; ○ Elevated) and 1998 (▲ Control; ■ Ambient; ● Elevated).

Growth under elevated CO_2 enhanced aboveground phytomass production (AGP) by 31% in 1997 and 47% in 1998 (Table 1). A trend in 1997 and significant differences in 1998 between control and ambient chamber AGP indicated greater production inside than outside of chambers. We suspect that warmer temperatures within chambers (about 2°C) caused earlier spring green-up and resulted in greater phytomass production in the chambers. An analysis of CO_2 growth responses of C_3 and C_4 grasses and forbs indicated no differences among these three functional groups in their above-ground growth enhancement from CO_2 enrichment (Morgan et al., 1998). These results indicate a strong growth enhancement of both C_3 and C_4 species in this semi-arid grassland, and support earlier growth chamber studies which showed significant photosynthetic and growth responses of C_3 and C_4 grasses from this system (LeCain and Morgan, 1998; Morgan et al., 1994; Hunt et al., 1996).

Growth in elevated chambers caused a 21% reduction in shoot N concentration and a 23% increase in shoot C/N ratio compared to ambient chambers, but had no affect on shoot C percentage. Plots of % shoot N and C/N ratios from both years as a function of above ground phytomass indicate good relationships between these traits and productivity (Fig. 1), although, not surprisingly, the relationships are different for green (July) and senescent (October) material. The July shoot samples have higher N concentration (0.97 %) compared to the senescent October samples (0.73 %), and consequently lower C/N ratios. Slopes also appear steeper for the summer data. Variation in aboveground phytomass in Fig. 1 is due to chamber and year affects in addition to CO_2 affects, and suggests that changes in plant N and C/N ratio which occur under elevated CO_2 may be largely due to dilution of plant nitrogen from stimulated growth.

Our results suggest increased productivity but lower forage N in future CO_2 enriched, warmer environments. The sustainability of these CO_2-induced growth enhancements will depend on soil N dynamics, a topic we are presently investigating.

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